ADAPTATIONS OF INSECTS TO SOIL DWELLING

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The soil consisting of three phases (solid, liquid and gaseous) has as an environment many peculiar properties. As the air in the soil is almost always saturated with water vapour, and films of water around solid particles are present, the conditions of existence in this medium are of intermediate character between aquatic and epigeion. Soil dwelling permits air respiration with the minimal water loss. So for many groups of terrestrial invertebrates the soil was a transitional medium in the course of their evolution from the aquatic to terrestrial habits (Ghilarov, 1944, 1948, 1949, 1956).

The physico-chemical régime of the soil determines the properties of soil dwellers, in particular of insects, differing from those of epigeion forms. Among the insects, Apterygote and Holometabolous larvae show the clearest adjustments to soil environment and are thus most suitable subjects for studies of the specificity of such adaptations. Adult Pterygota have developed their properties as adaptations to life in an aerial medium and, when transferring to soil dwelling, the secondary and incomplete character of such adaptations is always evident, whereas the main direction of nymphal evolution is an approach to the habits of the adults.

Differences between soil dwelling compared with an open mode of life on the soil surface become clear when studying morphological and physiological properties of soil insects, which in many respects are similar to those of aquatic organisms. High permeability of integument due to the insignificant development of epicuticle (in Onychiurids, Machilids, many larval Holometabola) is characteristic of soil dwellers. The cuticle permeability permits skin respiration in, e.g., tracheae-less Apterygota or *Tipula* larvae. It is noteworthy that naiads of Ephemerids and Odonata have well-developed, relatively impermeable epicuticle except on the tracheal gills. This proves the secondary character of their aquatic habits. In tracheate forms of soil dwelling Apterygota and larval Holometabola (as in air-breathing aquatic ones) the spiracles are open, lacking a closing mechanism (unlike epigeion insects).

The permeability of the cuticle for transpiration in soil insects makes them as sensitive to desiccation as aquatic invertebrates are. The cuticle of soil insects is permeable to dissolved salts too. By their diffusion rate through the cuticle of soil insects different ions may be arranged in the same sequence as for marine invertebrates. The cuticle permeability of soil insects determines their poikilosmy. In a temperate climate the cold resistance of soil insects is lower than that in insects living outside soil strata and shows smaller seasonal changes. With respect to cold resistance soil insects are intermediate between the remaining terrestrial and aquatic insects (the latter being of low cold resistance all the year round).

The relatively low cold resistance of many soil insects may be explained by the vertical gradient of temperature with its seasonal overturn in the soil (as in bodies of water too). This enables soil insects to choose the layer with the more favourable temperature.

Soil insects like many other pond dwellers are but little sensitive to the increased CO_2 concentration; the CO_2 content in soil air is higher than in the atmosphere, though lower than that dissolved in water of ponds and swamps.

Owing to the presence of water films in soil many soil insects (e.g. wireworms) are able to orientate themselves by gradients of dissolved substances. This ability is distinctive of true aquatic but not of epigeion terrestrial animals.

Saprophagy in soil insects is possible and widely distributed due to the presence of vegetable and animal remains undergoing decomposition through the fermentative action of micro-organisms. This nutrition type is common in aquatic animals (detritophagy) but not in true epigeion terrestrial ones.

The intermediate character of the soil as an environment is evident from the mode of insemination peculiar to soil Apterygota and other lower soil Arthropods. In aquatic invertebrates external insemination is very widely distributed, in epigeion terrestrial only internal insemination is possible, whereas the intermediate type—"externo-internal" insemination—is characteristic of soil Apterygota and other lower soil Arthropods. By the latter term the author means the mode of insemination when ejected sperm (or spermatophore) is simply dropped by the male in the external medium, and then picked up by the female. Such a mode of insemination is possible in soil Arthropods, because drops of sperm (uncovered or in permeable spermatophores) do not rapidly desiccate in air saturated with water vapour. The above properties show that soil insects differ essentially from the epigeion terrestrial ones in many respects. But nevertheless soil insects are typically air-breathing animals: wetting, presence of contact water in soil is unfavourable, even destructive for them, as has already been suggested by A. E. Cameron, 1913.

This double nature of soil insects—the combination of properties common to aquatic dwellers and terrestrial forms—is due to the remarkable properties of soil as an environment. The peculiarities of adaptations to soil dwelling leave their impression upon the mode of locomotion in this medium. The presence of interstices between not only solid particles but their aggregates as well and the ramifying network of root channels, cracks, etc., enables various types of locomotion in soil. For the minute Arthropods crawling in such passageways is possible in the same manner as on the solid substrate. Many insects using soil porosity for moving have sensorial cerci, enabling orientation by running backwards if facing barriers (e.g. Campodea, *Chlaenius*-larva). Larger insects use interspaces in soil only if they have a wormlike body, its flexibility being often due to the secondary segmentation (Cardiophorini, larval Therevidae). Some bigger larvae enlarge existing channels by propulsion, like earthworms (e.g. *Tipula*-larvae). Quite peculiar are adaptations of many larvae which have to move in the soil as a solid medium. Their anterior head margin, mouthparts or forelegs are adjusted to digging, adaptations for fixing the body when digging and propelling being also of value. Such fixation is attained by evolving fixing spines on the caudal end (e.g. *Selatosomus* and *Blaps* larvae) or by enlarging the supporting surface (e.g. C-shaped scarabaeoid larvae with folded soft bodies).

The latter types of adaptation do not occur in epigeion or aquatic insects; their evaluation as a kind of adaptation to the substrate surface (Dubois Reymond, 1911) is quite erroneous.

The above facts show that the soil is a very peculiar environment and merits recognition as an independent special medium of similar status to aquatic and epigeion terrestrial ones. To three "corpora naturae" distinguished by the famous author of "Systema Naturae", whose bicentenary we celebrate, the eminent Russian naturalist V. Dokutschaiev, founder of our pedology, reasonably added the fourth "natural body"—the soil. The founder of biogeochemistry V. Vernadsky also emphasized the soil as a special natural body. Nevertheless till now the majority of ecologists discriminate only "two major environments: terrestrial and aquatic" (vide G. L. Clarke, 1954, R. Hesse, 1924 *et al.*). But the flourishing of a new branch of biology—soil zoology—during the last few decades proves the soil to be quite a peculiar medium. It should be mentioned that the soil attracted the lifelong attention of the great Charles Darwin.

The present Congress celebrates the centenary of the scientific study of animal evolution; investigations of animal adaptations to soil dwelling elucidate the course of phylogeny in many branches of Regnum Animalium.

DISCUSSION

G. MARCUZZI: I think that the permeability of the cuticle of some soil inhabiting insects may be due to a secondary abrasion by the contact of the insects with hard soil particles, as has been demonstrated by Wigglesworth and his colleagues.

F. I. VAN EMDEN: I do not think that the views of Ghilarov and Wigglesworth are as irreconcilable as the discussion so far may suggest, as Wigglesworth was working with stored-product insects, which are exposed to evaporation for much of their life time, whereas soil insects are protected during much of their life by the high absolute humidity of their surroundings, if they have lost the epicuticle.

H. E. GOTO: Dr Ögel (Ankara University) demonstrated whilst working at Imperial College that at least one species of soil-dwelling Collembola (*Folsomia candida* Willem) possesses a distinct but fine epicuticle. This layer was demonstrated by electron-microscopy and by indirect evidence from survival times at different humidities after treatment with various adsorbents and abrasives followed by argentaffine test on the dead individuals. She showed that the epicuticle is abraded in nature soon after each moult and that adsorption of the waxes by clay and peat amongst other substances was more important than abrasion.

S. M. MANTON: I welcome Professor Ghilarov's view as to the primitive nature of a shallow soil-living habit for evolving terrestrial Arthropoda from aquatic ancestors. It is, however, clear that the ability to burrow, often deeply, in soil is made possible by specializations as great as those accompanying surface and aerial living. For example, J. G. Blower has demonstrated the presence of a thick lipoid layer over the cuticle of the deeper burrowers, Geophilomorpha and Juliformia, enabling these animals to resist osmotic uptake of water, in contrast to the Lithobiomorpha and Polydesmoidea; and I have shown how great are the trunk specializations of these animals which enable them to exercise their burrowing abilities by quite different means.